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It may be noted further that the acquisition of this new character by an originally non-saccharose-fermenting strain of B.coli has thus far developed only once and then on sodium chloride medium. Cultures of the parent organism grown in saccharose broth for a series of generations as yet show no gas production or acid production. This particular change therefore seems to be due to the intra-cellular or molecular changes brought about by non-specific influences and not to a direct adaptation to particular environmental conditions.

A DYNAMIC CONCEPTION OF THE ORGANIC INDIVIDUAL

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The organic world exists in the form of more or less clearly defined individuals, which may be completely isolated from others as self-maintaining organisms, or only partly isolated, like the members of a so-called colony among the lower animals and the different buds or growing tips and the parts associated with each in the multiaxial plants. A tree, for example, consists of a great number of plant individuals organically connected with each other.

In all except the very simplest organic individuals an orderly, definite sequence of events in space and time occurs which we call development. Development includes the series of changes from the reproductive cell or cell mass to the mature form of the organism. On the one hand, the organs arise in definite space relations to each other and to certain axes or planes which we can draw through the developing organism, and on the other hand, development consists in an orderly sequence of events in time. Certain regions always precede and others follow in regular order. The result of this orderly behavior is an organism of more or less definite form and structure, often exceedingly complex and with a high degree of constancy in successive generations. In the simplest individuals these space and time sequences are either less definite or else they are subject to frequent change and replacement by others, but in most organisms they are relatively permanent.

Most theories of the organism have failed to account satisfactorily for these orderly characteristics. Either they have simply assumed the existence of some sort of mechanism adequate to account for the facts, or some 'vitalistic,' i.e., non-mechanistic principle, as a controlling or ordering factor, or they have ignored the whole problem. Nevertheless, orderly behavior in development is one of the most fundamental and significant characteristics of the organism, for upon it depend the form and structure of the adult and the possibility of definite and coördinate function of parts.

During some fifteen years of experimental investigation of certain aspects of the problems of reproduction and development, I have been able to establish certain facts which throw some light on the problem of the mechanism which underlies the orderly character of development and at the same time point very definitely to certain conclusions concerning the nature of the so-called polarity and symmetry of the organism. Some of the more important of these facts and the conclusions drawn from them are briefly stated in the following paragraphs.

In all axiate forms (forms possessing one or more axes with reference to which an order is perceptible) which I have examined, including several species of ciliate infusoria, Hydra, and several hydroids, various flatworms, the eggs and developmental stages of several annelids, of starfish and sea urchin and of several fishes, and amphibia, there exists, at least during the earlier stages of development and in many cases throughout life, a gradient in rate of the metabolic processes or of certain fundamental metabolic reactions, which is coincident in direction with the longitudinal or chief axis of the body.[5, 7, 8, 9, 10] The region of highest rate in this gradient always becomes the apical region of the organism, i.e., the region which precedes in locomotion, or which is farthest removed from the region of attachment or insertion in the case of sessile forms, or is the chief region of growth or of reaction to external conditions according to the nature of the organism. Moreover, in those organisms in which a definite head appears, this head, or primarily the cephalic nerve ganglion which is its fundamental part and the first to appear in development, always arises from this region of highest metabolic rate.

This metabolic gradient can be distinguished in various ways; for example, the susceptibility of different regions of the body to various chemical agents such as the cyanides and at least many other narcotics in concentrations which kill in the course of a few hours, varies in general with metabolic rate.[6] Consequently when organisms and particularly the simpler forms and earlier stages of development, are killed by such substances a metabolic gradient appears as a death or susceptibility gradient, the regions of highest rate being most susceptible and dying first. Various other conditions such as lack of oxygen, high temperature, and in many cases low temperature also give the same death gradient and by means of the Tashiro biometer a gradient in CO_2-production in the same direction can also be demonstrated.

In much lower concentrations of the cyanides and narcotics which permit some degree of acclimation the susceptibility gradients of the organisms are reversed, because in these low concentrations the regions of high metabolic rate undergo more rapid and more complete acclimation to the reagent, while the regions of lower rate are less capable of acclimation and sooner or later die.

While the metabolic gradient along the longitudinal axis is usually the most clearly defined, similar gradients exist in relation to other axes or planes of symmetry. In at least most bilaterally symmetrical forms metabolic rate decreases from the median region laterally toward each side and in the invertebrates ventral regions have primarily a higher rate than dorsal, while in the earlier developmental stages of the vertebrates the metabolic rate decreases from the dorsal toward the ventral region. This difference between invertebrates and vertebrates is of interest in relation to the position of the postcephalic parts of the central nervous system, which in the former are usually ventral, in the latter dorsal.

When we examine the course of development in nature we find that it confirms these experimental results. In general, wherever we can distinguish an axis or a plane of symmetry we can distinguish a gradient or gradients in rate or sequence of development along the axis or in definite relation to the plane. This gradient corresponds in direction to the metabolic gradient and in all cases where a central nervous system appears, it is the first organ to become morphologically distinguishable, it arises from the region of highest metabolic rate in the primary gradients, and its cephalic part represents the region of highest rate in the whole organism.

There is also evidence that such metabolic gradients exist in plants, as well as in animals. Most plants are multiaxial forms, but as regards single axes, there are various indications of more or less definite metabolic gradients along these axes. We find, for instance, that the highest rate of growth occurs in the apical regions of each axis and that a more or less definite growth gradient extends from this region along the axis.

In general a relation of dominance and subordination exists between regions of higher and those of lower metabolic rate. If a region of high metabolic rate is once established in any way in an undifferentiated cell or cell mass a more or less definite gradient in rate extending to a greater or less distance from this region arises, because the changes in the primary region spread or are transmitted, but with a decrement in intensity or energy, so that at a greater or less distance from the point of origin they become inappreciable. It is evident that in general transmission of this sort must occur from a region of higher to one of lower rate of reaction, and S. Tashiro has found that this rule holds for the specialized form of transmission which is found in nerves. Thus the region of higher rate, once established, becomes an important factor in determining the rate of other regions, and since the rate thus determined is higher in regions nearer to it and lower in those farther away, a gradient results. Since the region of high rate of reaction determines the existence of the gradient, it becomes the chief factor in determining the rate of reaction in other regions within the range of its influence and therefore in determining the sequence of events in time and space in these parts. Consequently it appears to dominate or control other regions and they to be subordinate to it. It is evident that according to this conception the degree of dominance and subordination and the range of influence of the dominant part must depend primarily upon two factors. The first of these is the difference between the metabolic rate of the dominant part and the intrinsic rate of other parts before they were influenced by it. The higher the rate in the dominant region above the original intrinsic rate of the cell or cell mass the greater its effect in increasing the rate in other parts and the greater the distance to which its influence extends. The second factor is the efficiency of transmission. Where the transmitted changes influence other parts but slightly and soon die out, dominance is slight and limited to short distances from the dominant part, but where the decrement in the course of transmission is slight, as in the nerves of higher animals, the influence on the dominant part may make itself felt at very great distances.

I have been able to demonstrate experimentally in various ways this relation of dominance and subordination and to show that the axial gradient is an essential factor in determining the orderly formation of parts and their relations in space and time to each other. (For some of the experiments on *Planaria* see references 1, 3, 7. Various other data on coelenterates and flatworms are as yet unpublished.) For example, in the reconstitution of pieces of *Planaria* into new whole animals, the higher the metabolic rate in the developing head region, the farther away from the head do the pharynx and mouth appear, and vice versa, and other parts of the body show similar relations. Any piece of the planarian body is incapable of giving rise to any parts which are characteristic of levels of the body anterior to the level from which it was taken, unless a head first begins to develop. On the other hand, any piece is capable of producing parts characteristic of more posterior levels than its own, even in the complete absence of a head. These facts mean essentially that each level of the body is dominated by more anterior levels, but in their absence itself dominates more posterior levels and that the head region dominates all levels within a certain variable limit of distance.

It has also been shown by many authors that small isolated pieces of the body of various simple animals may undergo reconstitution into apical structures or heads without the presence or formation of any other parts of the body, but in no case has a posterior or basal structure arisen, except in connection with and as an outgrowth from more apical or anterior parts. In other words, the apical region or head of the organism is capable of developing independently and in the complete absence of other parts, while the formation of other regions of the body is dependent upon the presence of more apical or more anterior parts. This relation between apical or anterior regions and other parts is of fundamental importance for our conception of the organism, but, so far as I am aware, attention has not been called to its significance by those who have observed and recorded many of the facts.

In some of the lower animals it is even possible to eliminate experimentally the original gradient and then to produce a new gradient in the cell mass in a different direction. In such cases the original axis of the organism disappears and a new development takes place along an axis coincident with the newly established gradient, the region of highest rate in the gradient becoming the apical part of the new individual.

The dominance of the apical region, the growing tip, over other parts of the axis in the plants has long been known to botanists and it has been demonstrated repeatedly that this dominance can be decreased or eliminated and so the relations in space or time of other parts altered, by decreasing or inhibiting metabolic activity in the dominant region. Essentially the same relations undoubtedly exist along the axis in both plants and animals, but this very important fact has apparently not been recognized.

These and various other experimental data which cannot be mentioned here point us very definitely to the conclusion that the organic axis in its simplest form in both plants and animals is a gradient in rate of metabolism or of certain fundamental metabolic reactions, perhaps primarily the oxidations, and that such a gradient is at the same time the axiate organic individual in its simplest terms. In fact we may define the axiate individual as consisting primarily in a gradient or gradients in rate of metabolism or of certain metabolic reactions in a specific protoplasm. The organic individual is not then simply a hodgepodge of chemical substances: it is a physico-chemical complex with one or more reaction gradients. If this conception of the organic individual is correct, then we must admit further that physiological correlation is primarily a matter of the transmission of chemical changes rather than of the transportation of chemical substances. In other words, axiate organic individuation or integration is of the nervous type from the beginning, and the development of the nervous system is the morphological expression of physiological conditions which were present and began to act at the moment when the axis first arose and which in fact constitute the axis in its simplest terms. Undoubtedly specific chemical substances, hormones, products of metabolism, or whatever we prefer to call them, play very important parts in organic development, but the individual must already exist as an orderly whole before they can act in any definite and orderly manner.

We must now consider the question of the origin of the gradient, or more correctly of the region of high metabolic rate which determines the gradient. The only possible conclusion from many different lines of evidence is that it results from the differential action of factors external to the protoplasm, cell or cell mass concerned. We see gradients arising in nature in this way and it is possible to produce them experimentally. If this conclusion is correct, the so-called polarity and symmetry of organisms, which are in reality morphological and physiological expressions of these gradients, are not fundamental properties of protoplasm and do not result from polarities or symmetries of its constituent molecules or particles. They are therefore not comparable to the physical polarities and symmetries which are resultants of atomic or molecular constitution, for they represent molar differences in metabolic condition, which in the final analysis are of external origin. It is probable, however, that no cell or cell mass can continue to exist under ordinary natural conditions for any considerable length of time without acquiring at least a temporary gradient or gradients, for uniformity of action of external factors at all points of its surface is inconceivable, except perhaps for very short periods, and differences of action will result in a gradient or gradients. And it is certain that an orderly and definite sequence of events in time and space, such as occurs in organic development, is possible only where one or more of these metabolic gradients is present. Undoubtedly other factors besides the gradients play a part in determining the character of the results in many cases, but the orderly course of events is dependent upon the gradients.

The metabolic gradient cannot of course arise or persist simply as a gradient in rate of chemical reaction, for the metabolic processes and the colloid substratum, the protoplasm, in which they occur are always associated. The persistence of the gradient when once established, is due to the changes in the substratum connected with the differences in rate of reaction. For example, there is evidence that, at least in certain forms, a gradient in amount or activity of oxidizing enzymes exists along the axis.

According to this conception, the starting point of the process of differentiation is, in the final analysis, a quantitative gradient or gradients, i.e., a difference in rate rather than in kind of metabolic reaction. Is such a basis adequate? I believe it is. We know that in chemical reactions *in vitro* quantitative differences very often result in qualitatively different products. In the organism, where a great number of chemical reactions occur in a complex substratum which influences both their rate and character, the possibility of differences in quality arising from differences in quantity is much greater. The surface of the earth, with its physiographic features and its living forms, shows a remarkable differentiation along the equatorial-polar axis, and this differentiation results from the action of quantitative factors, viz., differences in light and heat. Moreover, it is possible to determine differences in the course and results of development which are manifestly qualitative by changes in external conditions which affect primarily the rate rather than the kind of reaction in the organism.

If the axiate individual is primarily a metabolic gradient or gradients, the lengths of these gradients represent the physiological limits of size of the individual. If the actual size exceeds this limit, either as the result of growth or of decrease in the length of the gradient, that portion which lies beyond the limit of size becomes isolated physiologically[2] This physiological limit of size is actually attained by the whole organism only in the plants and lower animals, where transmission is effective only over relatively short distances, because of the rapid decrement in intensity or energy. In the higher animals, where the chief conducting paths have become highly differentiated nerves, in which the decrement is very slight and transmission over very great distances is therefore possible, size is limited by other factors, such as the progressive differentiation of cells, which limit division and growth.

In the plants and lower animals the physiological isolation of a part usually results in reproduction of some sort, the character of the reproduction varying according to the conditions. Certainly the simpler and probably all agamic, or, as we commonly call them, asexual reproductive processes belong in this category, although additional factors are concerned in some. Reproduction under these conditions of physiological isolation means simply that the isolated part loses more or less completely its characteristics as a part, since the correlative conditions which determined them are no longer acting, and becomes a new individual, either with the persistence of the original metabolic gradients, or with the development of new ones through the action of external factors, both cases being represented in nature. We see these forms of reproduction very commonly in both plants and the lower animals. For example, in some of the worms, when the body attains a certain length, the posterior region becomes a new animal exactly as it does when we isolate it physically by cutting it off, and it can be shown that this reconstitution results from physiological isolation.[1, 4] In plants a new bud, which is a new plant individual, arises at a certain distance from the one previously formed, etc.

These reproductions have been variously controlled and modified in plants and I have found it possible to control them in animals. Growth is not necessary for their occurrence, for we can decrease the physiological limit of size of the individual, i.e., the length of the gradient, by decreasing the metabolic rate of the whole or of the apical region alone. One of the simplest ways of inducing such reproduction is to cut off the dominant region or decrease or inhibit its metabolic activity. This results in lowering the rate in all other parts and so in shortening the gradient, and this in turn results in physiological isolation of the more remote parts. Sometimes, when the gradient is nearly or quite eliminated, the individual breaks up into many new individuals, perhaps into single cells, each of which later repeats the process of development. Many cases of spore formation in the plants and lower animals are of this nature.

This conception of the organic individual throws light on many questions heretofore obscure. It not only accounts for the orderly behavior in space and time of the organism during development and for the agamic reproductions, but it enables us to understand how a multitude of axes or polarities, extending in all possible directions, can exist in different cells and organs at the same time with a general axis or axes of the whole organism.

This view also affords a basis for the interpretation and synthesis of the data of regeneration or form regulation which have stood heretofore as curious and remarkable facts, but without any adequate underlying general conceptions or working hypotheses. With this conception of the individual these data fall readily into line and many of them support and confirm it in a very definite way.

From this point of view the development of the nervous system as a conducting and correlating system and of its functionally dominant cephalic region are less completely mysteries than they have been, for we can see that they are the final results of conditions which existed at the first moment of individuation, and that the physiological integration of the organic individual is always fundamentally a relation of dominance and subordination. In the lower organisms and the earlier developmental stages of the higher, individuation approaches more or less closely to that type of social individuation which we find in the tribe or in certain forms of the primitive state, while in the later stages of development of the higher animals there are many indications of an approach toward democracy in the organism.

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